

ARENARIA, SECTION EREMOGONE (CARYOPHYLLACEAE)  
IN THE PACIFIC NORTHWEST:  
A KEY AND DISCUSSION

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*Arenaria* is one of the taxonomically most difficult genera in western North America. Members of Section *Eremogone* (the filiform-leaved cespitose perennials) are commonly encountered in the drier regions of the western United States. Although only 13 American species are normally recognized in this section, the group presents a vast and confusing array of morphological types. The present paper is an attempt to sort out and more completely describe the forms which occur in the Pacific Northwest and the ways in which they intergrade. An attempt is also made to summarize the evolutionary mechanisms by which such a species complex might originate. The study is an offshoot of a more comprehensive continuing investigation of the ecology and evolutionary history of species in the Cascade Mountains of Oregon (Hickman, 1968; Hickman and Johnson, 1969).

I have examined over 1000 specimens of eremogones from ORE, OSC, DS, and WSC. The fact that over 40 percent of these specimens were mislabeled or misfiled indicates the amount of taxonomic and nomenclatural confusion within the group. Specimens of all currently recognized North American species have been studied, but with minor exceptions type material has not been available. Strictly nomenclatural problems which would necessitate reference to types appear to be lacking. In addition to herbarium studies, all Pacific Northwest species, with the exception of typical *A. kingii* (Wats.) Jones, have been studied in the field.

All currently available treatments of this group (Maguire, 1947; 1951; Munz, 1959; Peck, 1961; St. John, 1963; Hitchcock, *et al.*, 1964) have some internal and mutual inconsistencies. Detail of treatment varies greatly, but only Maguire (1947) includes all five currently recognized Pacific Northwest species. In many cases the diagnostic characters cited by Maguire have proved too variable to be consistently useful.

The difficulties in arriving at a definitive treatment of the group include the fact that taxa of *Eremogone* are fully polythetic classes in the sense of Beckner (1959): they are sufficiently variable that no single set of characters will completely delimit them. Each population may have a large number of common characteristics, and every such character may be possessed by many members of the population but no single character is found in every individual. Each taxon represents a new combination of states of the numerous, widely-varying characters to-

gether with one or a few traits which are less widely distributed but which are nevertheless not always diagnostic. For example, the most definite character in this group of species is the sharply-pungent leaf tip of *A. aculeata* Wats. However, occasional specimens which on other grounds must be considered to be *A. capillaris*, *A. pumicola*, or *A. kingii* also have sharply-pungent leaf tips which are virtually indistinguishable from those of *A. aculeata*.

A taxonomic scheme for such a polythetic group based on the presence or absence of one or a few characters would be highly artificial, and natural separations must therefore depend on as large a number of characteristics as possible. There are so many intermediate forms that it is difficult, but necessary, to describe more fully material typical of the various species populations. The simple recognition of intermediate forms as such will be a great aid in working with this group floristically and taxonomically. For these reasons, a more completely descriptive key to these species is presented here. No new names or combinations are proposed at this time, but these will inevitably result from continued work with this complex genus. References for the original descriptions are available from standard taxonomic works, especially Hitchcock, *et al.* (1964).

Section *Eremogone* Fenzl. Plants perennial, frequently suffrutescent and more or less caespitose; capsule dehiscent by six teeth, each valve thus bidentate; leaves narrowly linear, obtuse to apiculate or acicular-pungent; glands at the base of the stamens conspicuous or occasionally obsolete.

#### *Key to Pacific Northwest Species*

Infl. congested, the fls. borne in one to several more or less capitulate cymes, glabrous; anthers white or yellowish; lvs. straight, thin, obtuse to apiculate, mostly 4–6 cm long; stems typically tall and leafy. Range: through e Oregon and Washington, e to Montana and Wyoming, s to southern Colorado, Nevada, and the s Sierra Nevada. The most widespread and variable taxon.

*A. congesta* Nutt.

Infl. an open cyme, normally glandular (rarely glabrous); lvs. various, but if straight under 3 cm long.

Basal lvs. persistent, recurved (in material from Nevada, lvs. often straight and strictly ascending); herbage, at least in dried specimens, appearing permanently dusty from the translucent cuticle and occasional very short eglandular hairs; infl. glabrous to densely but minutely glandular. Range: in pure form, from Harney and Malheur cos., Oregon, e across s Idaho to sw Wyoming, and s through the Great Basin; in forms intermediate to *A. capillaris americana* at least as far north as Gilliam and Morrow cos., Oregon. . . . *A. kingii* (Wats.) Jones (in the Pacific NW var. *glabrescens* Mag. = *A. aculeata* Wats. var. *uintahensis* (Nels.) Peck).

Basal lvs. persistent or falling in age, rigidly ascending, lax, or curved in the same direction; not recurved; herbage glaucous (especially the basal lvs.) or glabrous; infl. glandular-pubescent.

Lvs. with long-subulate, yellow, pungent tips; basal lvs. rigid-ascending in youth, arcuate-spreading in age, strongly persistent, normally under 2 cm long; cauline lvs. above the lowest pair abruptly reduced and mostly scarious; stems strongly matted. Range: the Wallowa Mts. e through c Idaho to sw Montana, s and w to ne California, n Nevada, and nw Utah. . . . . *A. aculeata* Wats.

Lvs. with green, acute to apiculate, non-pungent tips.

Basal lvs. thick, rigid-ascending, glaucous, never spreading or curved, falling after one or two years leaving a naked, incompletely lignified caudex that branches just below the soil surface; cauline lvs. markedly wider than the basal, somewhat fleshy, of equal size up to the many-flowered infl. Range: in pure form, from Marion Co., Oregon, s in the Cascades to Crater Lake, occasional in the Siskiyou Mts. as far w as Curry Co., Oregon. Intermediates between this and *A. capillaris americana* are found from the Three Sisters, Lane Co., n to Whatcom and Okanogan cos., Washington. (The variety *californica* Maguire, with less fleshy lvs. and woodier caudex, is found in the Sierra Nevada from Sierra to Mono cos. It is transitional to *A. kingii*). . . . . *A. pumicola* Cov. & Leib.

Basal lvs. thin and somewhat lax, all lvs. of one vegetative stem curved slightly to markedly in the same direction, glabrous, toothed along the margins, persistent at the base, 2.5–4 cm long except for alpine ecotypes, where shorter; stems somewhat matted; cauline lvs. of same shape as basal, not fleshy, reduced gradually to the relatively few-flowered infl.; anthers purple. Range: Alberta and British Columbia s in the Cascades to the Three Sisters, Oregon, and in the Rockies to Montana and c Idaho. Found occasionally in the Columbia Basin in forms transitional to *A. congesta*. *A. capillaris* Poir. subsp. *americana* Maguire (= *A. formosa* of American authors, not *A. formosa* Fisch.)

The present treatment has a number of limitations. Although the diagnostic character sets have been made as large as possible, the characters (as previously noted) are not always faithfully associated. It will remain unclear which characteristics can be considered most nearly diagnostic until exhaustive experimental work is undertaken.

Sepal shape, a character heavily weighted by most workers in this genus, has not been included in the present key because of the great variability within single flowers and more importantly because of the

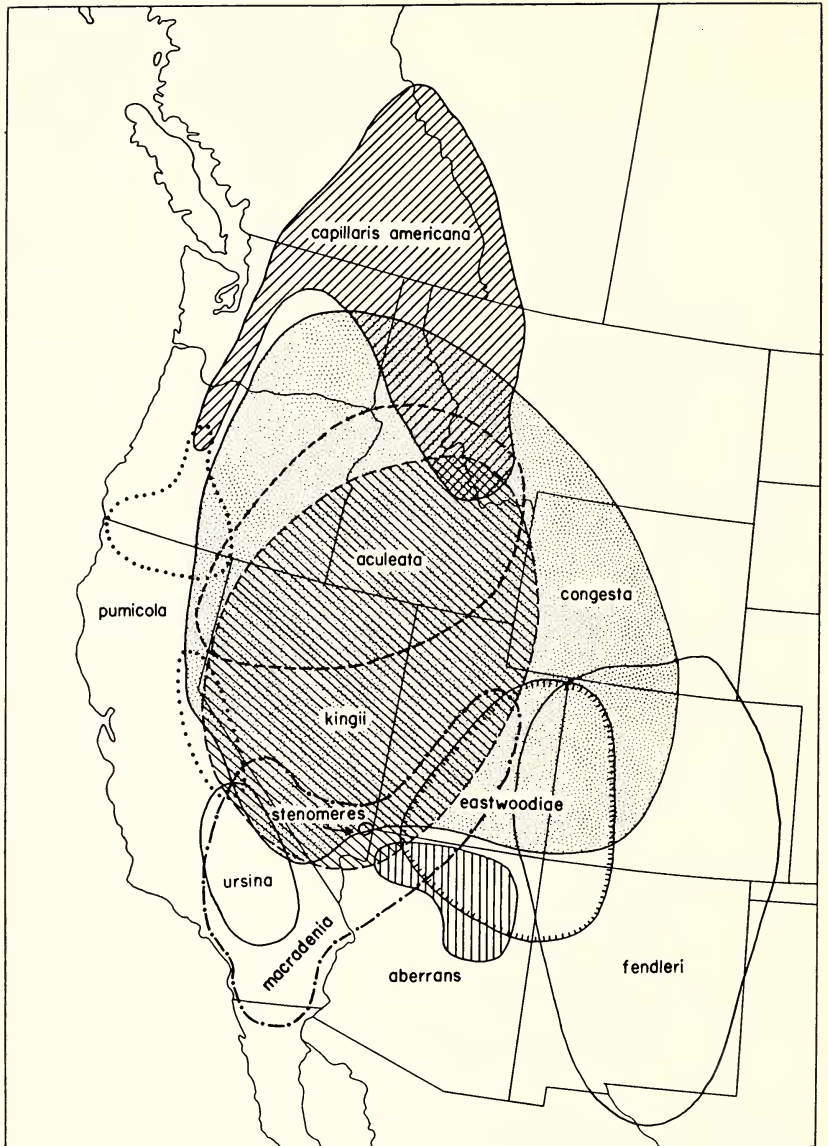


FIG. 1. Geographical distributions of eleven taxa of *Arenaria* (*Eremogone*) in western North America.

lack of any discontinuities in the clines of this character. There is no doubt a correlation between sepal shape and some of the characteristics used above, but the relationship is too complex to be incorporated usefully into a key. In general, *A. capillaris*, *A. aculeata*, and *A. pumicola* have obtuse or barely acute sepals; the sepals of *A. congesta* vary from

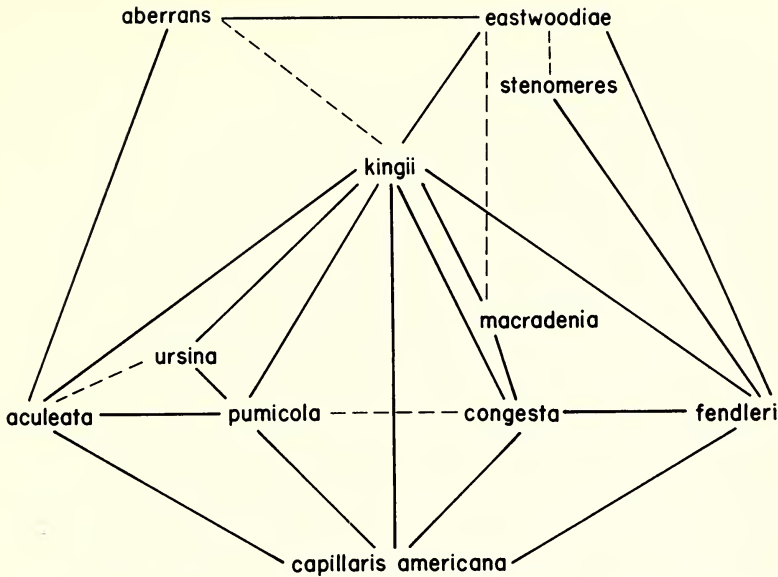


FIG. 2. Morphologically derived patterns of intergradation among eleven taxa of *Arenaria* (*Eremogone*). Dotted lines indicate less obvious affinities.

obtuse to acuminate; and *A. kingii*, throughout most of its range, but not in Oregon or western Idaho, has definitely acute sepals.

While I have studied some material of all 13 American species of *Eremogone*, most was collected from the Pacific Northwest. Due to the gradually shifting nature of the diagnostic features of all the taxa when they are considered throughout their ranges, the present key will decrease in value with distance from this region. However, for all of Oregon, Washington, Idaho, Montana, and large portions of California, Nevada, Utah, and Wyoming, the five species treated here are the only ones encountered (fig. 1).

*Arenaria franklinii* Dougl. and *A. hookeri* Nutt. have been excluded from this study because they seem intermediate between Sections *Eremogone* and *Alsine*, having the capitate inflorescence of *A. congesta* and the prostrate habit of *A. nuttallii* Pax. *A. franklinii* is found throughout eastern Oregon and in adjacent Washington, Idaho, and Nevada; and *A. hookeri* occurs primarily east of the continental divide in Montana, Wyoming, and Colorado.

*Arenaria capillaris americana* intergrades morphologically with all of the other species treated here (fig. 2, which shows morphologically derived estimates of present or past gene flow among the 11 species). The only character that is reliable in separating this species from *A. congesta* is the congested inflorescence. Six Pacific Northwest varieties of *A. congesta* have been characterized by more open inflorescences and combinations of other highly variable characters. It is my opinion that these

“varieties” represent intermediate forms with *A. capillaris americana* in our range, and elsewhere with other taxa—especially *A. fendleri* in Wyoming and Colorado and *A. macradenia* in southern California, Nevada, and Utah. It is also possible that a very small number of genes is involved in producing a congested inflorescence in this genus and that this characteristic has arisen numerous times in various parts of the section.

Other intermediates are also common. Robust forms of *A. capillaris americana* from lower elevations between the Three Sisters and Mt. Hood, and highly reduced alpine forms from Mt. Hood to northern Washington exhibit the wide, somewhat fleshy cauline leaves characteristic of *A. pumicola*. *Arenaria capillaris americana* partially intergrades with *A. aculeata*, since many sharply pungent-leaved specimens show some signs of leaf length and laxness characteristics of the former species. It also merges completely with *A. kingii glabrescens*, resulting in the occurrence of *capillaris*-like morphological characters as far south as White Pine Co., Nevada. Occasional intermediates between *A. aculeata* and *A. kingii* have been collected in southeastern Oregon; and one population from Gearhart Mt., Lake Co., Oregon, is intermediate between *A. aculeata* and *A. pumicola*. As mentioned in the key, *A. pumicola* var. *californica* appears to be derived from typical *A. pumicola* and *A. kingii*.

The diversity of intermediate forms suggests that barriers to gene exchange in these species are incomplete. In addition, there is considerable evidence here for a complex pattern of reticulate evolution. *A. capillaris americana* is apparently the most primitive member of the section discussed here, providing the North American connection between the circumboreal *A. capillaris* subsp. *capillaris* and the more southerly derived species. *Arenaria capillaris* is the only American species found north of the southern limit of Pleistocene continental glaciation. With considerable recombination possible, there has been great potential for local differentiation as the migrating complex has come into contact with new environments. Fluctuating climates from the late Tertiary to the present have no doubt had the following three important and recurring effects: 1, isolation of relatively small populations; 2, re-establishment of contacts between formerly isolated populations; 3, re-isolation of local populations following gene exchange with other types. Such processes could easily have led to the observed widespread complex of interrelated forms, the larger units varying gradually with geographic locality. These mechanisms could also explain the broad areas of “specific” overlap shown in Fig. 1. At present there are virtually no ecological data from which one might deduce the importance of character displacement in functionally separating populations of *Eremogone* in areas of sympatry, but this must be considered as an alternative suggestion.

*Arenaria kingii* seems to comprise the central portion of the complex,

both morphologically and geographically. This species also contains the most diverse and incongruous forms and is partially sympatric or parapatric with all other American eremogones. It seems likely to me, by means of the evolutionary-migrational mechanisms outlined above, that this species has been a "genetic dumping ground" for all the closely related taxa. It may either represent the parental stock or be derived by recombination from many of the more localized entities. Probably both hypotheses are in part correct, but verification of this will prove difficult. If only the latter is correct, the biological validity of *A. kingii* as a species could be questioned, but, as pointed out by Maguire (1947), to discard the name would cause insurmountable problems in the taxonomy of the section. The central morphological tendencies of *A. kingii* are illustrated in Fig. 2.

This discussion of evolutionary patterns is highly speculative, but is suggested by the trends of various morphological characters. Work by others is beginning to elucidate genetic and chromosomal patterns in some portions of the section. Extensive experimental studies are needed to assess the biological significance of the described morphological patterns and to support or contradict the derivative evolutionary hypotheses presented here. Until such studies are completed, these impressions will be of value to those who wish to understand eremogones from the Pacific Northwest as the species are presently constituted.

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